a multistage process. If pre- and post-isolating mechanisms are part-and-parcel of an inevitable evolutionary drive towards taxonomic overspecification, then they should be treated as such in all their fascination, and not as part of an inclusive defining moment.

So, where do we go from here? After all, we all know and love species. They are the units of functional cohesion of populations of similar individuals that are the focus of our research programmes. The path to take, according to Mallet, is to provide, as a minimalist objective, a definition that does not confuse process with pattern. For this he proposes the 'genotypic cluster definition', meaning that collections of genetic and phenotypic markers that are collectively shared by a group of individuals, and which are not shared with other groups (recognized through their own shared clusters), would constitute a species.

I have two problems with this: one trivial and one non-trivial. First, Mallet wishes to discriminate between the 'genotypic cluster definition' and the 'phenotypic species concept' of Cracraft, which is based on the supposed necessity of apomorphies. As Mallet points out, the resolving power of molecular techniques is capable of providing individual specific apomorphies, so getting us nowhere. Clusters of apomorphies shared by individuals (essentially the genotypic cluster definition) might seem to get around this problem but it still doesn't provide a workable guide as to how we isolate a species from the lower and higher taxonomic units. And indeed, why should we bother if, as Darwin argues, species are functionally compatible. At the heart of sex is the idea that many species share very similar key biological functions but that the precise molecular manner in which such functions are brought into effect differ between species. In other words, while molecules A and B in one species and A1 and B1 in another are compatible with each other, interspecific mixtures of A and B1 and A1 and B are not compatible. Hence, A and B have the essential capacity to coevolve (often the result of an interaction between natural selection and molecular drive4,5). By such means, key biological functions are maintained while species differentiation proceeds. Molecular coevolution and its emphasis on the functional interactive biology of genes is but one example of the types of phenomena we should be exploring if we are to understand the dynamics of speciation. A major headache ahead of us but ultimately tractable. From such studies, a functional species definition will emerge by rights.

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References

Mallet recently transcribed the so-called biological species concept (BSC) in a logically superior way under the heading 'genotypic cluster definition' (without providing a definition as such). He pointed out that the BSC is not a product of the Modern Synthesis but much older. I cannot agree more, and would like to add that mid-19th-century practising malacologists even predated the authors cited by Mallet. For example, the evolutionist Mousson2 wrote (in German): 'The species is the total of individuals, interconnected by descent and reproduction, maintaining unreduced reproductive capacities' (p. 13). He recognized polytypic species ('Formenkreise') and emphasized the difference between sympatric and allopatric occurrences: systematists should investigate 'whether or not the forms of a single area are interconnected by all possible intermediate forms and ways of life, and whether forms of different areas, followed topographically, gradually change into each other ... (pp. 7–8).

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References

Reply from J. Mallet

Many 'good' species hybridize in nature - about 10% of animals such as birds and butterflies1,2 and even more among plants3. Even the largest animal that has ever existed, the blue whale (Balaenoptera musculus) hybridizes successfully with the fin whale (B. physalus)4. A definition of species based on interbreeding, like the BSC, simply isn't practical. In addition, the BSC runs into theoretical difficulties when used in tests of hypotheses of speciation, because the assumption of species cohesion via gene flow makes speciation appear more difficult than necessary5.

So the BSC and other assumption-laden definitions, such as the recognition, cohesion and phylogenetic concepts, are neither useful in practice nor in evolutionary theory. Instead, we must accept that species are man-made groupings whose importance to us is operational; species do not necessarily define themselves by means of an underlying biological 'essence'. The belief that definitions need to be based on 'concepts' rooted in the true 'essence' of the thing to be defined dates from Plato and Aristotle, and was revived by Hegel, who is much admired by Mayr6. The rest of modern science, meanwhile, now avoids essentialistic definitions7. For example, nobody argues about definitions of stars: a star is simply a very massive object that emits light. A number of evolutionary biologists have recently realized that species can be better defined by modifying Darwin's operational definition to include genetic evidence8. A suitable definition (supplied and demonstrated in my TREE article, despite Gittenberger's assertion to the contrary) is that species are groups that remain recognizable in sympathy because of the morphological and genotypic gaps between them. This kind of species is free to hybridize in theory as well as in practice; and can evolve via reticulation, as well as in the strictly hierarchical mode assumed under the phylogenetic concept. It is curious, therefore, that Gittenberger accuses me of having
Spatial dynamics and chaos

In their TREE review, Bascompte and Solé examine the population dynamics consequences of explicitly incorporating the spatial dimension into ecological models. A major argument advanced is that 'complex movement is enhanced by dispersion' and to support this assertion, Bascompte and Solé refer to examples of diffussion-driven chaos\(^2,3\). It is well known that in continuous-time models, at least three variables are necessary for the emergence of chaotic oscillations; this requirement is relaxed with the inclusion of spatial degrees of freedom\(^4,5\). This destabilizing mechanism does not transfer to discrete-time models, however, whereas chaos can be observed in even the simplest one-dimensional models\(^6,7\). While there are some extreme cases of dispersal having a destabilizing influence\(^6,8\), it has been shown that spatial coupling usually does not alter the stability properties of a discrete-time system\(^9,10\). This is in direct contrast to the claims of Bascompte and Solé who, based mostly on their own research\(^11,12\), propose that equilibrium stability decreases as the spatial domain is increased - a phenomenon which they call a spatially induced bifurcation.

The findings of Bascompte and Solé's earlier work\(^1,12\) arise solely as a result of biologically impossible assumptions embedded within their models\(^13,14\). Phrased as discrete analogues of reaction-diffusion equations, their models ignore the processes of competition and dispersal on the same individuals. While in reaction-diffusion models (which concern infinitesimal rates of change) this assumption is valid, in discrete-time and discrete-space models, it can lead to the same individuals dying and yet dispersing; this mechanism is also responsible for the generation of negative population densities in their models. Bascompte and Solé have argued elsewhere\(^15\) that their formalism is intended to reflect a scenario where individuals compete for resources and then disperse within the same life-stage. When an individual-based model is employed to explore this situation (thus avoiding the pitfall of generating negative densities), the stability boundaries of the model remain unaffected by dispersal\(^16\).

In conclusion, while Bascompte and Solé's review is both interesting and very timely, some of the results they present are contradicted by other studies, and have been shown to depend critically on the specific (and controversial) fashion in which their models are formulated.

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References


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References


Reply from J. Bascompte and R.V. Solé

The above comment is the latest round in a running argument about a technical subject (dispersal) in which the way in which it is formulated and how it affects local dynamics, we are afraid that such comment does not add to the published discussion, and we suggest that readers refer to previous discussion\(^2,2\) or even our own review in TREE\(^3\) where we tried to addresses all of this controversy (see our Box 2).

We agree with Rohani and Ruxton that some of the modelling approaches used by us are a little simplistic, and that the role of dispersal in local dynamics can depend on the specific dispersal rule. Further work is necessary, as we emphasized in our prospects section. However, Rohani and Ruxton adopt an extreme position. Their statement that our previous results emerge solely as a result of unrealistic dispersal rule should be tempered. The references cited in their comment relating to our early work describe many results as the emergence of spatial patterns or the coexistence of competitors mediated by space, which have been found simultaneously by other authors using other modelling rules (see references in Tree\(^2\)).

When Rohani and Ruxton refer to the specific issue of diffusion-induced chaos, claiming that such a destabilising mechanism does not transfer to discrete models, their statement should again be tempered. As pointed out recently in this journal in a reply to Ruxton's first comment\(^4\) by Hastings and Higgin, the extensive study of a discrete time model shows unequivocally that spatial degrees of freedom 'allowed for even more complex behaviour to emerge than was found in models that did not incorporate spatial dynamics\(^5\). Furthermore, this result was obtained adopting the dispersal rule used by Rohani and colleagues\(^6\).

To sum up, the comment by Rohani and Ruxton is useful in exploring more realistic scenarios, in adopting a critical re-examination of results, and in suggesting further studies. At the moment,